Neonatal Face To Face Interactions Promote Later Social Behavior In Infant Rhesus Monkeys

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Abstract

In primates, including humans, mothers engage in face-to-face interactions with their infants, with frequencies varying both within and across species. However, the impact of this variation in face-to-face interactions on infant social development is unclear. Here we report that infant monkeys (*Macaca mulatta*) who engaged in more neonatal face-to-face interactions with mothers have increased social interactions at 2 and 5 months. In a controlled experiment we show that this effect is not due to physical contact alone: monkeys randomly assigned to receive additional neonatal face-to-face interactions (mutual gaze and intermittent lipsmacking) with human caregivers display increased social interest at 2 months, compared to monkeys who received only additional handling. These studies suggest that face-to-face interactions from birth promote young primate social interest and competency.

Key terms: sociality, social development, mother-infant interaction, visual attention, eye tracking, individual differences

Introduction

Highly social species, including human (*Homo sapiens*) and nonhuman primates (NHPs), evolved a variety of socio-cognitive skills and behaviors – including complex facial expressions, grooming, and play – that facilitate cooperation amongst group members[1]. In these societies, characterized by complex and extended social interactions, social competency is critical for survival and reproductive fitness[2]. However, the mechanisms by which individuals acquire social competence early in development are not well understood.

One mechanism proposed to support early social development is face-to-face interactions[3, 4, 5]. Face-to-face interactions between newborns and caregivers occur across many human cultures[6, 7], and have also been reported for some NHPs (e.g., chimpanzees, *Pan troglodytes*[8]; Japanese macaques, *Macaca fuscata*[9]; rhesus macaques, *Macaca mulatta*[3]), especially during or following physical separation[3, 5, 8, 10]. In NHPs, face-to-face interactions include mutual gazing (MG), which is often accompanied by facial gestures such as lipsmacking[3]. Similar to humans[11, 12], NHPs show considerable variability in face-to-face interactions with newborns[3, 5, 8], and there is evidence that disruption of the mother-infant bond in rhesus monkeys negatively impacts infants' social and physiological development[13]. One possible mechanism for this disruption is the lack of face-to-face interactions between mother and infant. Primates, including humans, are attracted to the eye region of faces from the first weeks of life[14, 15], and prefer direct gazes to other visual stimuli[16, 17, 18, 19]. In infant rhesus

monkeys, increased visual attention to the eyes is associated with other social skills such as neonatal imitation[15]. Face-to-face interactions offer opportunities for the infant to learn key information about the caregiver, about species-specific interactions, and about the foundations of early emotional communication[3]. However, what remains unclear is the extent to which sustained face-to-face interactions and their variability influence the expression of social behavior later in development.

We addressed this question by studying the effects of neonatal MG on the later social behavior of infant rhesus monkeys, a highly social Old World primate species with strong mother-infant bonds and social complexity in adulthood[20]. We predicted that, if MG is a primary driver of the development of social skills, then monkey infants who receive more MG should be more social later in development. To test this prediction, we first observed naturally-occurring variation in mother-infant face-to-face interactions (see Supplementary Movie 1) to determine whether the quantity of face-to-face interactions predicts infants' later developing social behavior (Experiment 1). In this study, we focused on face-to-face interactions that occurred during close physical proximity because it was not possible to observe such interactions when monkeys were out of contact (see Methods). We then carried out a second study in which infants were randomly assigned to receive varying levels of face-to-face interactions (see Supplementary Movie 2) and physical contact with human caregivers in a controlled rearing environment (Experiment 2). Thus, through a combination of both naturalistic observations and experimental manipulations we were able to gain a more complete

picture of the contributions of neonatal MG to the developing infants' social interest and engagement in social behaviors. We report here that infants experiencing more face-to-face interactions in the first month of life exhibit more social interest at 2 and 5 months, suggesting that face-to-face interactions from birth promote young primate social competency.

Results

Results from studies of semi free-ranging monkeys

In Experiment 1, we studied MG in semi free-ranging rhesus monkey mothers and infants (N=10) living in a large, 2-ha enclosure. Researchers recorded the frequency of MG between mothers and infants across the first three months of life[5], and tracked infants' social behavior (i.e., social play, close proximity to other monkeys, and grooming) for the first 5 months of life (see Methods). Infants who engaged in MG more frequently with their mothers in the first month of life were more sociable later on: they spent more time in social contact with other monkeys at 2 months of age (Spearman correlation; $r_{(s)}$=0.68; p=0.031; Fig. 1a), and they initiated more social interactions at 5 months of age (Spearman correlation; $r_{(s)}$=0.78; p=0.007; Fig. 1b). Infants did not preferentially initiate social behaviors with their mothers; instead they initiated social behaviors with all types of partners: other adults, other infants, juveniles, and their mothers.

Results from studies of monkeys in a controlled environment

In Experiment 2, infants were reared in a nursery by human caregivers and had continual contact with peers[21]. Mother-infant physical contact can promote social behaviors[22, 23], which may be driving the increased sociality observed in Experiment 1. We therefore carried out a second study to determine the extent to which increased physical contact *or* increased face-to-face interactions influenced later social behavior. We randomly assigned infants to receive standard care (*N*=17), increased handling by human caregivers without face-to-face contact (caretakers' faces were covered; *N*=15), or both increased handling and face-to-face interactions (MG and intermittent lipsmacking; *N*=16), for the first 4 weeks of life[24] (see Methods). We then tracked infants' social development with two measures across the first 5 months of life: 1) by assessing infants' preference for a social (i.e. a macaque mother with her infant being groomed by another adult) vs. non-social (i.e. geometric shape) videos using an eyetracker, and 2) by measuring social behavior during infants' daily interactions with same-aged peers.

Infants who experienced additional face-to-face interactions spent more time at 2 months of age looking at the social stimulus than the non-social stimulus (paired-sample t-test; $t_{(15)}$=2.38; p=0.031, d=0.55, Fig. 2a), whereas infants who experienced handling-only or standard-care exhibited no preference (paired-sample t-test; handling-only: $t_{(14)}$=0.837; p=0.416; standard-care: $t_{(16)}$=0.446; p=0.661, Fig. 2a). At this age, we also found a significant effect of face-to-face interaction on the amount of time infants spent in social interaction with peers (ANOVA; $F_{(2,40)}$=4.125; p=0.023, η^2=0.141; Fig. 2b):

infants in the face-to-face condition spent more time interacting with peers (mean ± SD = 157.5s ± 36.4s) than infants in the handling-only (mean ± SD = 125.4s ± 45.4s; $t_{(29)}$=2.133; p=0.042, d=0.78; post-hoc t-tests) or standard-care groups (mean SD = 117.1s; $t_{(31)}$=2.567, p=0.016; d=0.92; post-hoc t-tests). There was, however, no difference in social behavior between the handling-only and standard-care groups ($t_{(29)}$=0.48; p=0.635; post-hoc t-tests). Although surrogate-peer-reared infants engaged in social interactions for significantly longer (153.3s ± 38.1s) than peer-reared infants (ANOVA; 117.3s ± 47.7s; $F_{(1,40)}$=7.956, p=0.007, η^2=0.136), there was no significant effect of the interaction between treatment group (face-to-face + handling, handing-only, standard-reared) and nursery rearing condition (peer-reared, surrogate-peer-reared) (ANOVA; $F_{(2,40)}$=1.138, p=0.331). These findings indicate that the effect of the stimulation on infant social behavior is not driven by any specific rearing condition. Finally, it is possible that the infants in the face-to-face condition were more likely to seek social contact with their peers because they experienced higher levels of anxiety. However, we did not find any effect of the face-to-face condition on rates of self-scratching (ANOVA; $F_{(2,40)}$=0.361, p=0.699), time spent ventral clinging on peers (ANOVA; $F_{(2,40)}$=2.170, p=0.127), or time in contact with the surrogate (ANOVA; $F_{(2,40)}$=1.080, p=0.349), suggesting that the effect of face-to-face interaction on social behavior is not due to the infants seeking reassurance from their peers or to a generalized reduction of anxiety. No group differences were observed on either measure at 5 months of age.

Discussion

Our combined observational and experimental studies demonstrate that, in both a naturalistic and a laboratory setting, early face-to-face interactions between newborn primates and their caregivers significantly affect infants' social behavior later in development: monkeys engaging in more face-to-face interactions as newborns spend more time in social contact with conspecifics, look longer at social stimuli, and initiate more social interactions. These effects do not appear to be due to increased physical contact between the newborn and caregiver, but appear to be driven by face-to-face interactions.

Interestingly, it has been reported that the frequency of mother-infant mutual gaze not involving lipsmacking predicted the amount of lipsmacking that the infants received from their mothers[3]. Moreover, lipsmacking by adults to infants coincides with mutual gaze[3], suggesting that in order for lipsmacking to occur, mutual gaze must be occurring. While these events are difficult to record in the field, as they require close proximity and detailed video microanalysis, this and other studies suggest they are more common in nonhuman primates than previously thought[3,5], and they probably have a significant impact on infants' affective and cognitive development, as also proposed in humans[25, 26]. Further studies are needed to assess which specific component of mother-infant face-to-face-interactions play a crucial role in the development of infant macaques social skills.

All infants, including those who are not exposed to a high rate of lipsmacking from their own mothers, are likely to experience these mutual interactions with other individuals of the social group, which may explain why infants who were not observed to receive face-to-face interactions with their mothers do not show gross social dysfunctions. This seems particularly true after the first month of life, when such mutual exchanges between macaque mothers and infants dramatically decrease[3]. Indeed, typically-reared infant rhesus macaques become more independent after their first month of life, when their interest in and proximity to same-age peers and other individuals within the troop steadily increase[27]. By six months of age, infants typically spend the majority of their daytime hours away from their mothers and engaged with peers in social interactions[27].

Previous work demonstrated that infant monkeys randomly assigned to receive more face-to-face interactions (mutual gaze and lipsmacking) were more likely to imitate facial gestures at one week of age, compared to infants who did not receive these additional interactions[24]. The present findings suggest that these face-to-face interactions may have even longer-lasting effects on infant social behavior beyond the newborn period. However, the controlled experiment revealed no significant effects of the face-to-face interaction on social behavior with peers beyond the second month of life, while the field experiment showed effects at five months. This discrepancy is likely due to the fact that in the field face-to-face interactions between mothers and infants continue well beyond the first month of life[5]. In contrast, in the controlled setting, the intervention only lasted for the first month of life. It is likely that continuing the face-to-face interactions would

193 have resulted in longer-lasting social effects in the nursery group as well.

194

195 There was considerable natural variability in the extent to which mothers in the field
196 interacted with their infants: only about half of the mothers were observed engaging in
197 these face-to-face interactions, consistent with previous reports[3, 5, 8]. Those infants
198 whose mothers were not observed to engage in face-to-face interactions with them
199 nonetheless went on to develop normally. That is, there did not seem to be any obvious
200 dysfunction in these mother-raised infants as a function of not having high rates of
201 mutual gaze with their mother as neonates, at least during the first 5 months of life.
202 Furthermore, because we did not observe such interactions it does not mean they did
203 not occur; interactions may have occurred at times in which they were not observed or
204 may have been subtle or difficult to detect in this context. Nonetheless, these findings
205 suggest that for some dyads, such mother-neonate interactions may be quite rare, and
206 perhaps there may be other causes of variability in these interactions besides human
207 interference (for example, maternal experience and infant sex[5]).
208 It is not yet clear what the mechanisms are underlying the differential social behavior for
209 infants receiving variable early caregiving. One possibility is that variability in face-to-
210 face interactions may modulate the activation of the oxytocin system[28], as oxytocin is a
211 neuropeptide that plays a key role in mother-infant bonding and promotes affiliative
212 relationships[29] and that may influence downstream social development[30]. Recent work
213 has shown that endogenous oxytocin in children can be increased through parental
214 contact[29] and that exogenous oxytocin increases eye contact in humans with and

without autism[31]. It is therefore possible that different levels of oxytocin in infants and/or in caregivers influence the frequency of face-to-face interactions, or vice versa, which might ultimately promote differential levels of social engagement[29]. In support of this, aerosolized oxytocin increases affiliative behavior in newborn macaques, especially among infants with stronger social skills, suggesting oxytocin may amplify infants' intrinsic social interest[30].

Our data suggest that the development of sophisticated social interactions and complex social systems might have been an important factor driving the evolution of mother-infant social gazing. Individuals living in a stable social group need to employ advanced social skills both to coordinate their own behaviors with the behaviors of other group members, and to solve direct and indirect conflicts that originate from competition over resources[32]. The primate species in which mutual gazing has been reported to date, namely macaques (e.g. rhesus macaques[3]; Japanese macaques[9]), geladas (*Thereopithecus gelada*[33]), chimpanzees[8], and humans[10, 11], are all highly social species characterized by multi-male multi-female social systems. Interestingly, in these species, individuals use social tactics to secure access to resources and increase their reproductive success[34, 35]. We suggest that, in these species, the acquisition of social skills starts in infancy, since being able to learn these skills from caregivers through, for instance, face-to-face interactions promotes social competence, which is critical for survival in adulthood in complex societies[32].

Methods

All procedures were approved by the NICHD Animal Care and Use Committee.

Experiment 1

Rhesus monkey mother-infant dyads (*N*=10; 4 male infants) were born and raised at the Laboratory of Comparative Ethology's 5-acre field station and the NIH Animal Center in Poolesville, Maryland. We studied dyads in the birth seasons (spring and summer) of 2013 and 2014. This semi-free ranging population of approximately 80 monkeys has been well characterized[5, 36]. Mothers and infants were undisturbed for the duration of the study.

Three observers recorded mother-infant interactions, trained to >85% reliability according to the methods detailed by Ferrari and colleagues[3, 5]. We conducted live focal animal observations[5, 37] between 0900 and 1700, 1-2 times per day, 5 days per week for the first 30 days of the infant's life; 3 times per week during days 31-60; and once per week during days 61-90. We coded dyads for 15 minutes, and sessions were coded from the infant's perspective. We discarded sessions if the focal animals moved out of sight or if either the mother or infant fell asleep for over 50% of the session[5]. We recorded the frequencies of mutual gazing, defined as eye-to-eye contact between mother and infant lasting at least 3 seconds (see Supplementary Movie 1), in each 15-minute session.

We observed infants from days 30-180 for all occurrences of behaviors using focal animal observations[5, 37]. From days 30-60, infants were coded twice per week for 20 minutes each session; from day 60 onward infants were coded weekly for 30 minutes each session. We recorded behaviors on a MobileDemand xTablet T7200 (Hiawatha, Iowa, USA) using JWatcher software[38]. For this study, the following behaviors were coded as initiated or received by the infant:

1. Social play: Play face, non-aggressive chasing, tagging, swatting, bobbing, biting, pulling, lunging, mouthing, or wrestling (rough and tumble) directed toward another animal.
2. Social contact: In physical contact or within arm's reach of another animal.
3. Social grooming: Cleaning/picking/stroking hair.

We calculated the average rates of mutual gazing between mother and infant for the first month of life. We calculated average durations and frequencies of each of the social behaviors for each month between 2-6 months. We used Spearman correlations to relate mutual gazing with durations of each of the behaviors at each month of age. Additionally, we calculated a composite "initiate social" score for each month (i.e., from 2 to 6 months) by averaging the durations of all social behavior (social play + social contact + grooming) that the infant initiated. We again used Spearman correlations to relate mutual gazing with the initiation of social behaviors at each month of age. We ran these latter correlations for interactions between infants and all other social partners,

and for interactions between infants and separate classes of social partners (i.e., mother, adult female, adult male, juvenile, other infant).

Experiment 2

Infant rhesus macaques (*N*=48; 27 males) were raised in a nursery from the day of birth following established procedures in our laboratory[30, 39, 40]. For unrelated projects, some infants (*N*=28) were reared in groups of four (peer-reared), while others (*N*=20) were reared in single cages outfitted with cloth-covered surrogates and given daily 2hr play sessions (surrogate-peer-reared), beginning at approximately 40 days of age. Prior to this time infants were housed in an incubator for the first 14 days of life, then transferred to a single cage until group formation. The single cages were all contained in the same room so that infants had constant visual and auditory contact with one another.

On the day of birth, we randomly assigned infants to one of three conditions. In two of these conditions infants received additional daily stimulation: a face-to-face + handling condition (FF, *N*=16) and a handling-only (HDL, *N*=15) condition. We compared these stimulated infants to a standard-reared control group (SR, *N*=17), who received no additional social interactions beyond standard rearing[39, 40]. Each stimulation session was carried out by one of approximately a dozen different caregivers, so that infants did not form an attachment to any one experimenter.

In the FF condition, a human caregiver attempted to engage the infant in mutual gaze and, upon doing so, directed lipsmacking gestures (LPS) at the infant for approximately 5 seconds, followed by a 10-second neutral still-face period (see Supplementary Movie 2). This LPS-still period was repeated every 30 seconds, for a total face-to-face interaction lasting 5 minutes per session. We chose LPS because it is a common, affiliative behavior mother rhesus macaques direct to their infants during face-to-face interactions[3] and infants imitate LPS in the first week of life[40]. In the HDL condition, a human caregiver held the infants for the same duration (5 minutes), but wore a face cover to prevent the infants from seeing the caregiver's face. For the first two weeks of life, we administered both FF and HDL four times per day (at ~10 am, ~12 pm, ~2 pm, and ~6 pm) during weekdays and twice per day on the weekend (at ~10 am and ~12 pm). In the third week of life, we administered FF and HDL three times per day (at ~10 am, ~12 pm and ~2 pm) and once per day on weekends (at ~10 am), while in the fourth week of life we administered FF and HDL twice per day (at ~10 am and ~ 12 pm) during weekdays and once per day on weekends (at ~10 am). The purpose of this gradual reduction in sessions was to prevent infants from growing accustomed to regular stimulation that would end abruptly, and to mimic naturally-occurring declines in mother-infant face-to-face interactions across development[3].

At 40-50 days of age (median=41 days), we tested infants in an eyetracking task to assess preference for social interactions. We recorded infants' eye movements via corneal reflection using a Tobii T60XL (*n*=38) or a Tobii TX300 (*n*=10) eye tracker and a

sampling rate ≥60 Hertz. We used Tobii Studio software (Tobii Technology, Sweden) to collect and summarize the data.

One experimenter held each infant ca. 65 cm in front of the screen, swaddled in a soft blanket. We calibrated each infant using a 5-point calibration to Tobii Studio's pre-set locations. Infants viewed one 30-second video (see Supplementary Movie 3) that depicted a social monkey scene on one side (a macaque mother with her infant being groomed by another adult) and a non-social scene on the other side (abstract shapes continuously moving across the screen). Location of the social scene was counterbalanced (left/right) between infants. We repeated the task when infants were 149-246 days (median=161 days); one infant was not re-tested at this older age for non-experimental reasons.

We observed infants in their social groups (i.e., during play sessions in the case of peer-reared infants) twice per week, once in the morning and once in the afternoon, using 5-minute focal animal sessions[37]. We recorded the following interactions:

1. Social contact: When the infant was either in physical contact or in close proximity (within arm's reach) of a peer.
2. Play: play behaviors that included play face, non-aggressive chasing, tagging, swatting, bobbing, biting, pulling, lunging, mouthing, wrestling (rough and tumble).
3. Social grooming: Cleaning/picking/stroking hair.

4. Self-scratches: Raking one's own hair or skin with fingernails including large movements of arm**.**

5. Ventral clinging: Ventral contact with peers.

6. Surrogate: time spent inside the surrogate.

We collected data on self-scratching, ventral clinging and time spent in the surrogate, as these are considered reliable indicators of anxiety[41].

For the eye-tracking task, *w*e drew areas of interest (AOI) for each side of the screen. We extracted total fixation durations using the Tobii filter in Tobii Studio (velocity: 35 pixels per window; distance threshold: 35 pixels). We calculated a preference score for the social video [social / (social + non-social)] and compared the amount of time infants looked at the social versus the non-social stimuli using a paired-sample *t*-test.

For social interactions, we created a composite social score by taking the average time infants spent in social contact, play and grooming. This social score, as well as mean rates of self-scratching, ventral clinging and time spent in the surrogate were calculated at two different time points: 1) at two months (i.e., between 36 days, when infants were first introduced to the social group, and 60 days) and 2) at 5 months (i.e., 121-150 days). We could not include two infants (one in the FF and one in the SR condition) at two months, because they were introduced to the social group when they were older than two months. For each time point, we ran one-way ANOVAs that included the

behavior of interest as dependent variable, with condition (FF, HDL, SR), rearing (peer-reared, surrogate-peer-reared) and their interaction as independent variables, and post-hoc *t*-tests to conduct pair-wise comparisons.

Data Availability Statement

The authors declare that the data supporting the findings of this study are available within the article's supplementary files (Supplementary Data 1 and 2).

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Acknowledgements

Supported by NICHD Division of Intramural Research and NICHD grant PO1HD064653 (P.F.F.). We are grateful to the animal care and veterinary staff at the NIH Animal Center.

Author Contributions

A.M.D. designed Study 1. P.F.F., E.A.S., A.P., and V.S. designed Study 2. A.M.D., K.L.B., and A.M.M. collected data for Study 1, led by A.M.D. E.A.S, V.S., A.P., K.L.B., A.M.M., M.M., N.M., G.M., and S.S.K.K. carried out the neonatal interventions in Study 2, lead by E.A.S. A.P. and G.M. collected eyetracking data in Study 2. K.L.B., M.M., and N.M. carried out behavioral scoring for Study 2. A.M.D. and S.S.K.K. analyzed the data and produced the graphs. A.M.D., S.S.K.K., E.A.S., A.P., and P.F.F. drafted the manuscript. S.J.S. and P.F.F. provided resources for the studies. All authors edited and approved the final version of the manuscript.

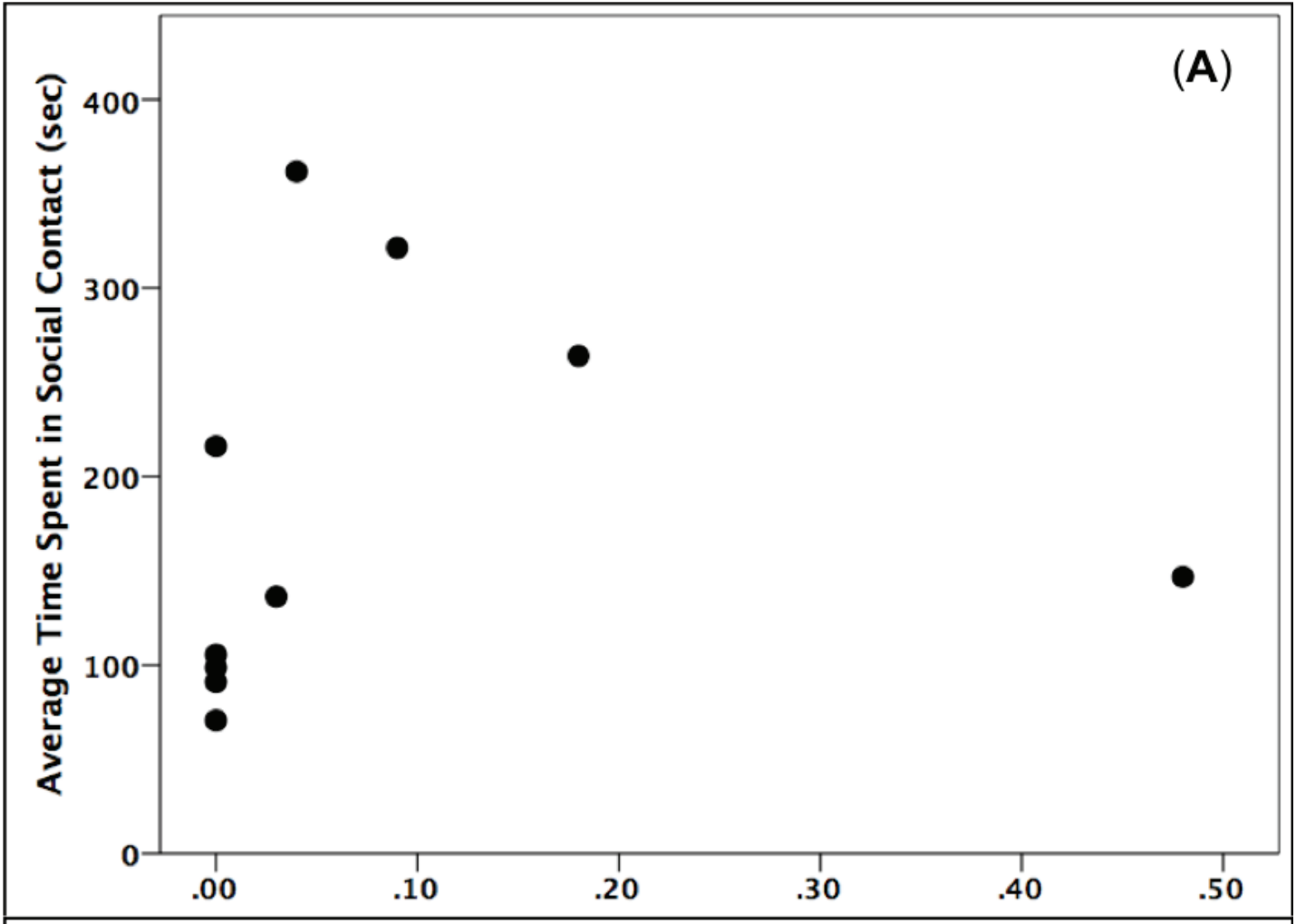
Competing financial interests

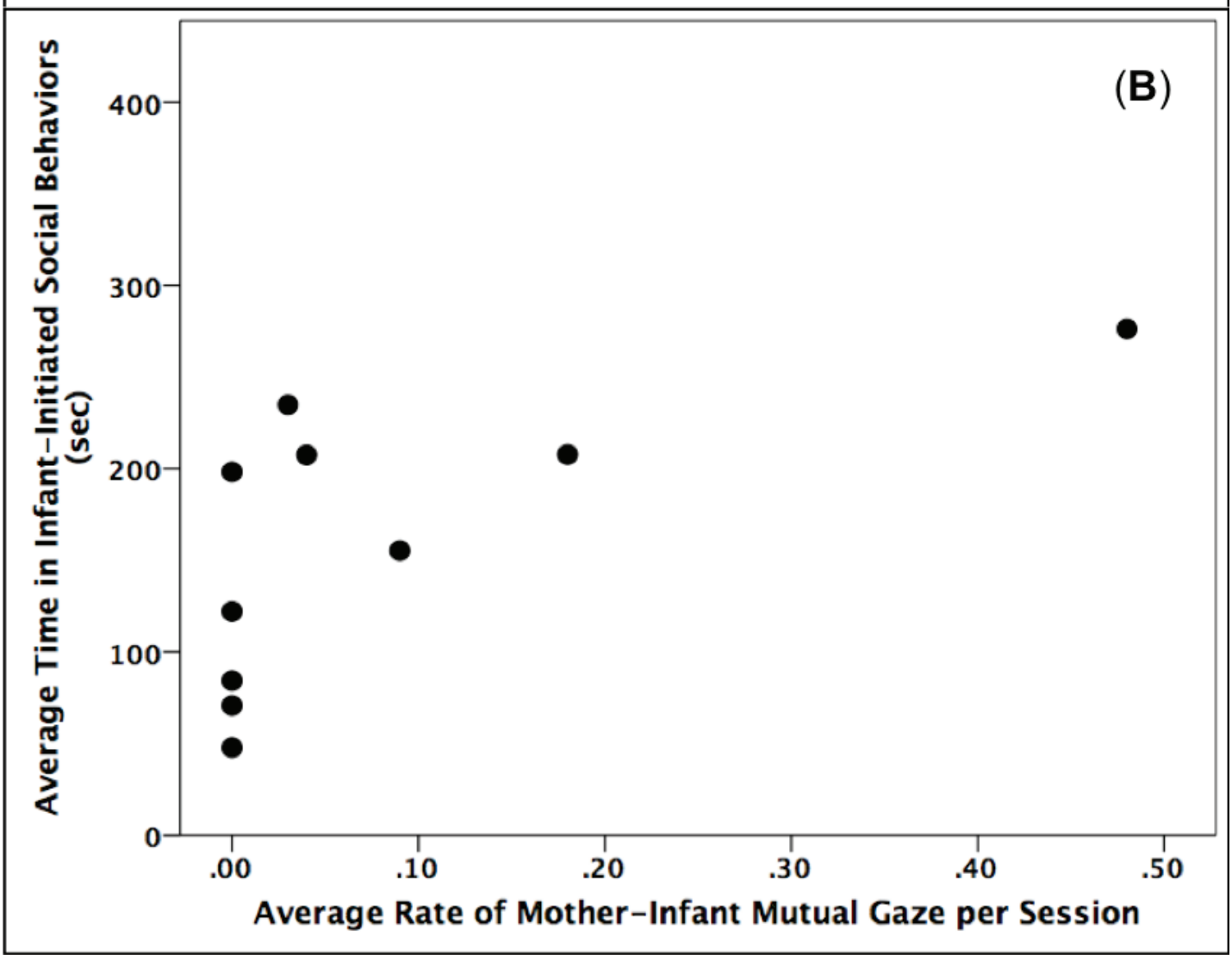
The authors declare no competing interests.

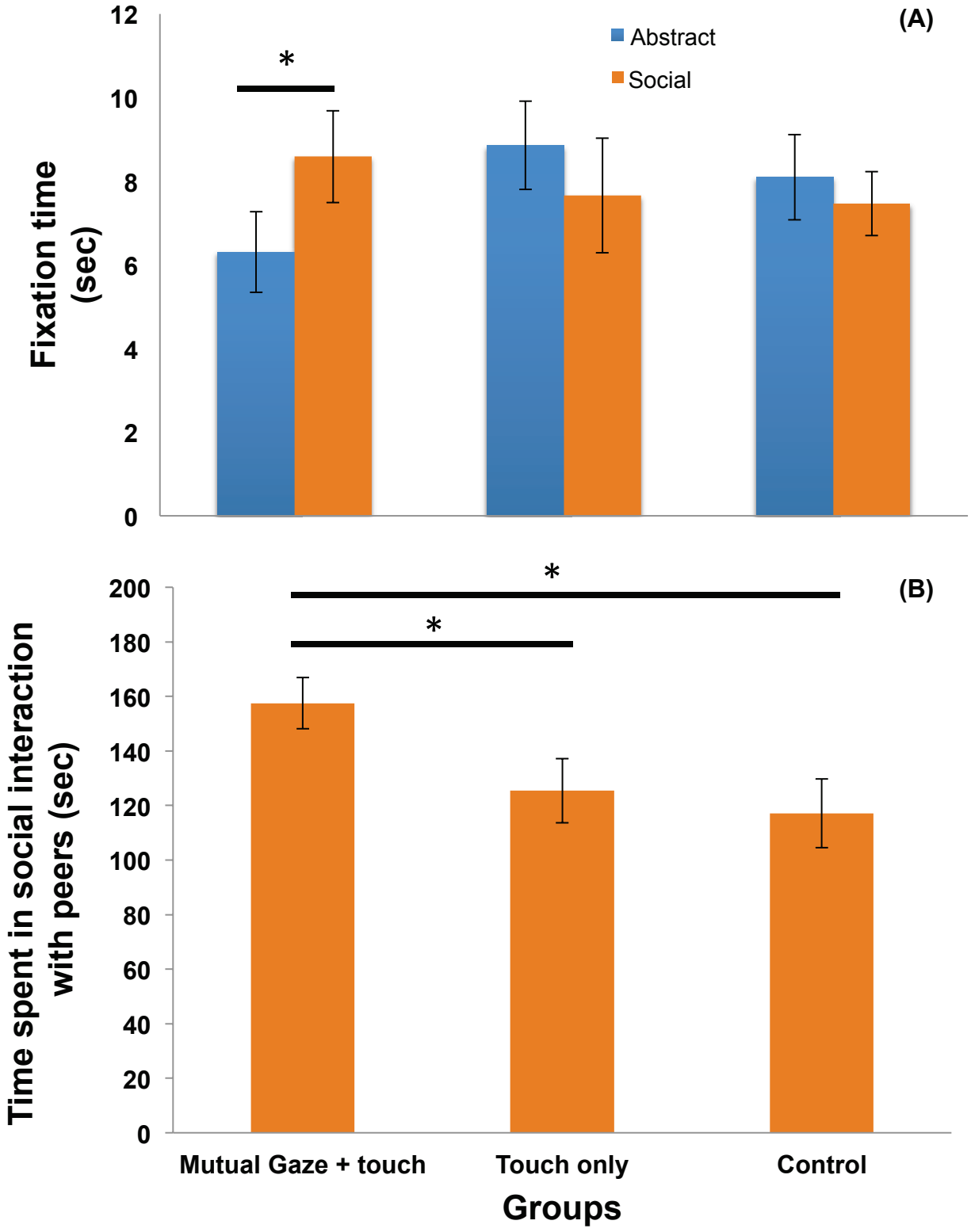
Figure Legends

Figure 1. How mother-infant face-to-face interactions influence infant social behavior. Results from Experiment 1 examining neonatal mother-infant face-to-face interactions and later infant social behavior. (**a**) Correlation between rates of mother-infant mutual gazing in the first month of life and time the infant spent in social contact at month two. Rate of gazing=total frequency of mutual gaze in first 30 days/total number of 15-min sessions in first 30 days. *N*=10. (**b**) Correlation between rates of mother-infant mutual gazing in the first month of life and time infants spent in social behaviors (e.g., groom, play, social contact) they initiated. Rate of gazing=total frequency of mutual gaze in first 30 days/total number of 15-min sessions in first 30 days. *N*=10.

Figure 2. **Face-to-face interactions, but not extra handling, influence social development.** Results from Experiment 2: (**a**) Effect of face-to-face + handling treatment on average time looking at social (orange) vs. nonsocial/abstract (blue) stimuli during the eyetracking task at two months, and (**b**) effect of face-to-face + handling treatment on average time spent in social contact with peers at two months. Face-to-face + handling, *N*=16; Handling, *N*=15; Standard-care, *N*=17. *p<0.05. Error bars reflect SEM.


(A)
Average Time Spent in Social Contact (sec)
400
300
200
100
0
.00
.10
.20
.30
.40
.50


(B)
Average Time in Infant-Initiated Social Behaviors (sec)
400
300
200
100
0
.00
.10
.20
.30
.40
.50
Average Rate of Mother-Infant Mutual Gaze per Session


(A)
Abstract
Social
*
Fixation time (sec)
12
10
8
6
4
2
0
(B)
*
*
Time spent in social interaction with peers (sec)
200
180
160
140
120
100
80
60
40
20
0
Mutual Gaze + touch
Touch only
Control
Groups